

POSTFIRE CHAPARRAL REGENERATION UNDER MEDITERRANEAN AND NON-MEDITERRANEAN CLIMATES

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ABSTRACT

This study compares postfire regeneration and diversity patterns in fire-prone chaparral shrublands from mediterranean (California) and non-mediterranean-type climates (Arizona). Vegetation sampling was conducted in tenth hectare plots with nested subplots for the first two years after fire. Floras in the two regions were compared with Jaccard's Index and importance of families and genera compared with dominance-diversity curves. Although there were 44 families in common between the two regions, the dominant families differed; Poaceae and Fabaceae in Arizona and Hydrophyllaceae and Rosaceae in California. Dominance diversity curves indicated in the first year a more equable distribution of families in Arizona than in California. Woody plants were much more dominant in the mediterranean climate and herbaceous plants more dominant in the bimodal rainfall climate. Species diversity was comparable in both regions at the lowest spatial scales but not at the tenth hectare scale. Due to the double growing season in the non-mediterranean region, the diversity for the first year comprised two different herbaceous floras in the fall and spring growing seasons. The Mediterranean climate in California, in contrast, had only a spring growing season and thus the total diversity for the first year was significantly greater in Arizona than in California for both annuals and herbaceous perennials. Chaparral in these two climate regimes share many dominant shrub species but the postfire communities are very different. Arizona chaparral has both a spring and fall growing season and these produce two very different postfire floras. When combined, the total annual diversity was substantially greater in Arizona chaparral.

Key Words: Climate, dominance, fire, species diversity, spring and fall annuals.

Chaparral is a fire-prone evergreen shrubland that is the dominant vegetation in the mediterranean-type climate (MTC) region of California (Keeley 2000). From a global perspective this vegetation is somewhat unique in that it not only tolerates frequent fires but many of the species have fire-dependent reproduction, similar to shrublands in other mediterranean-climate regions (Rundel 1981; Keeley and Bond 1997; Keeley et al. 2005).

Chaparral shrublands, however, are not restricted to MTCs as this vegetation type is widely distributed in southwestern USA and disjunct to northeastern Mexico (Keeley and Keeley 1988). Arizona mirrors the MTC in the winter rains that taper off to a late spring drought, but departs from the MTC by addition of a second rainy season in the summer. However, the importance of summer rains to the dominant shrubs is a matter of some debate, as it appears that these rains play a minor role in shrub growth and reproduction (Vankat 1989). Northeastern Mexico has a winter drought and summer rain climate, but the physiological responses of the shrub dominants to drought are remarkably similar to Californian shrubs (Bhaskar et al. 2007).

Arizona chaparral covers more than two million hectares (Schmutz and Whitham 1962; Bolander

1982) and occurs in widely disjunct patches from near Prescott in the northeast to the southeastern mountains around Tucson and east to the southwestern edge of New Mexico (Cable 1975; Pase and Brown 1982; Whittaker and Niering 1964, 1965). Arizona and California are broadly similar in the shrub dominants that are shared between these two regions (Knipe et al. 1979). Northeast Mexico chaparral is restricted to patches of severe substrate in the Sierra Oriental Mountains south of Monterey, and this vegetation shares some of the same shrub species and genera as the Arizona and California chaparral communities.

The Arizona and Mexican chaparral are of interest for what they can potentially tell us about the evolution of chaparral taxa. Paleoecological studies have suggested that many chaparral shrub species originated in interior portions of the southwest (Wolfe 1964, Axelrod 1989) and contemporary populations in Arizona and northeastern Mexico are interpreted as remnants of a Tertiary chaparral like vegetation that comprises taxa that largely originated under non-mediterranean type climates (Ackerly 2009; Keeley et al. 2012).

Although postfire chaparral responses have been studied in great detail in the winter rain region of California, little is known about

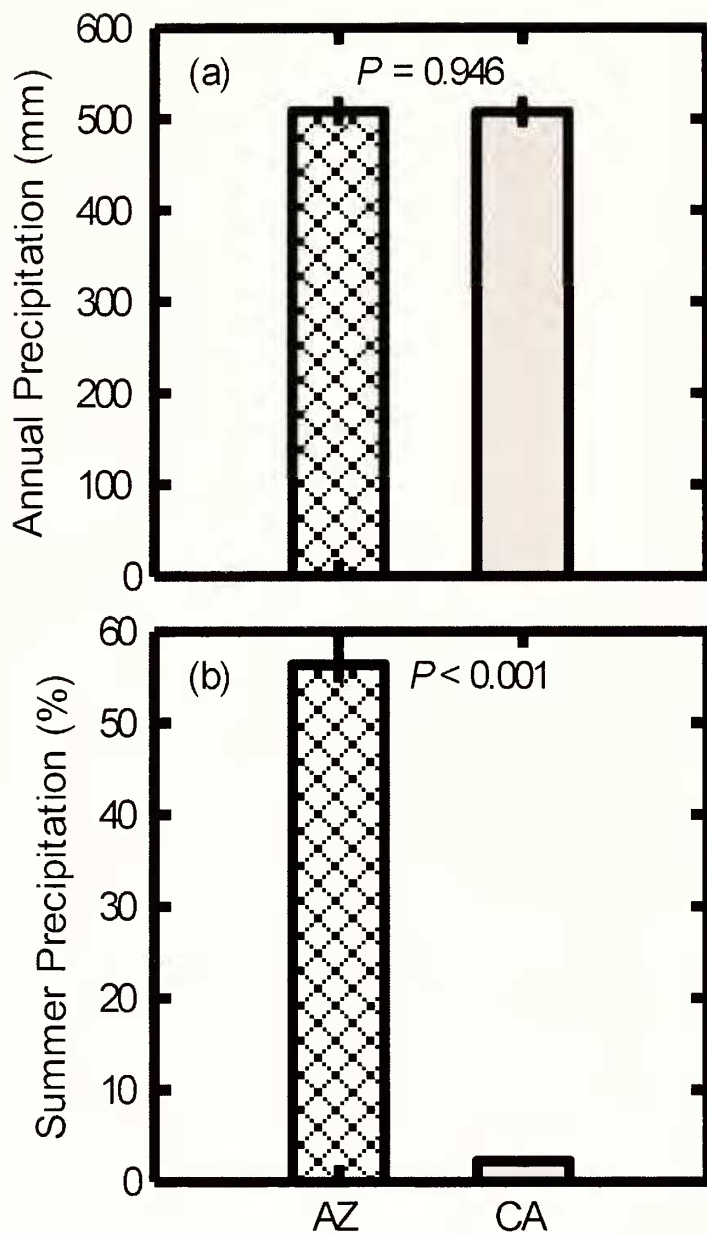


FIG. 1. Patterns of (a) long-term average annual precipitation and (b) proportion falling during the 'summer' rainy season (defined as July, August and September) for the nearest stations to the Arizona (AZ) and California (CA) study sites used in this project. Error bars are the standard error of the mean.

community responses in the bimodal rainfall region of Arizona. Postfire regeneration of Arizona chaparral has largely focused on shrub responses with relatively little attention to community responses and regeneration strategies of other life forms (Pase and Pond 1964; Pase 1965; Carmichael et al. 1978).

The purpose of this study was to contrast postfire recovery in the MTC California chaparral with postfire recovery in the non-MTC Arizona chaparral. We utilized data from studies of 2003 wildfires in California (same sites as in Keeley et al. 2008) and from studies of 2002 wildfires in Arizona (same sites as in Fotheringham 2009).

METHODS

Study Sites

The Arizona sites were burned in the late spring and summer of 2002 and were distributed across six fires in southeastern Arizona and southwestern

TABLE 1. FIFTEEN DOMINANT PLANT FAMILIES IN ARIZONA AND CALIFORNIA POSTFIRE CHAPARRAL SITES BASED ON AERIAL COVERAGE.

State/family	Normalized cover
Arizona	
Poaceae	1.00
Fabaceae	0.676
Asteraceae	0.327
Verbenaceae	0.138
Fagaceae	0.100
Molluginaceae	0.085
Convolvulaceae	0.074
Liliaceae	0.055
Malvaceae	0.054
Euphorbiaceae	0.043
Geraniaceae	0.032
Boraginaceae	0.025
Agavaceae	0.025
Rhamnaceae	0.018
Krameriaceae	0.016
California	
Hydrophyllaceae	1.00
Rosaceae	0.704
Cistaceae	0.345
Ericaceae	0.319
Fabaceae	0.254
Convolvulaceae	0.240
Rhamnaceae	0.237
Liliaceae	0.228
Asteraceae	0.174
Boraginaceae	0.168
Fagaceae	0.163
Poaceae	0.143
Papaveraceae	0.094
Scrophulariaceae	0.092
Fumariaceae	0.089

New Mexico (Fotheringham 2009). This study included 40 sites that were selected based on evidence of chaparral vegetation present prior to fire, fire size, range of fire severities, and accessibility, and were sampled in the first two postfire years. Sites were grouped by fire for analysis, except due to the small size and proximity of the Merritt and Ryan fires these were grouped together, and due to the large size of the Bullock Fire these were separated into two groups, the lower elevation Bullock and the higher elevation Upper Bullock. California sites were from five fires that burned in autumn 2003 and included 250 sites that were dominated by chaparral prior to the fires and sampled over the first two years; due to their proximity, the Grand Prix and Old fires were analyzed as a single fire. Both Arizona and California fires were distributed across a range of about 150–200 km but the former were distributed at about the same latitude in a west to east gradient and the latter along a north to south gradient (see Keeley et al. 2008 and Fotheringham 2009 for detailed maps). Chaparral sites studied in Arizona were at significantly higher elevation (AZ sites = 1620 m, CA sites 785 m).

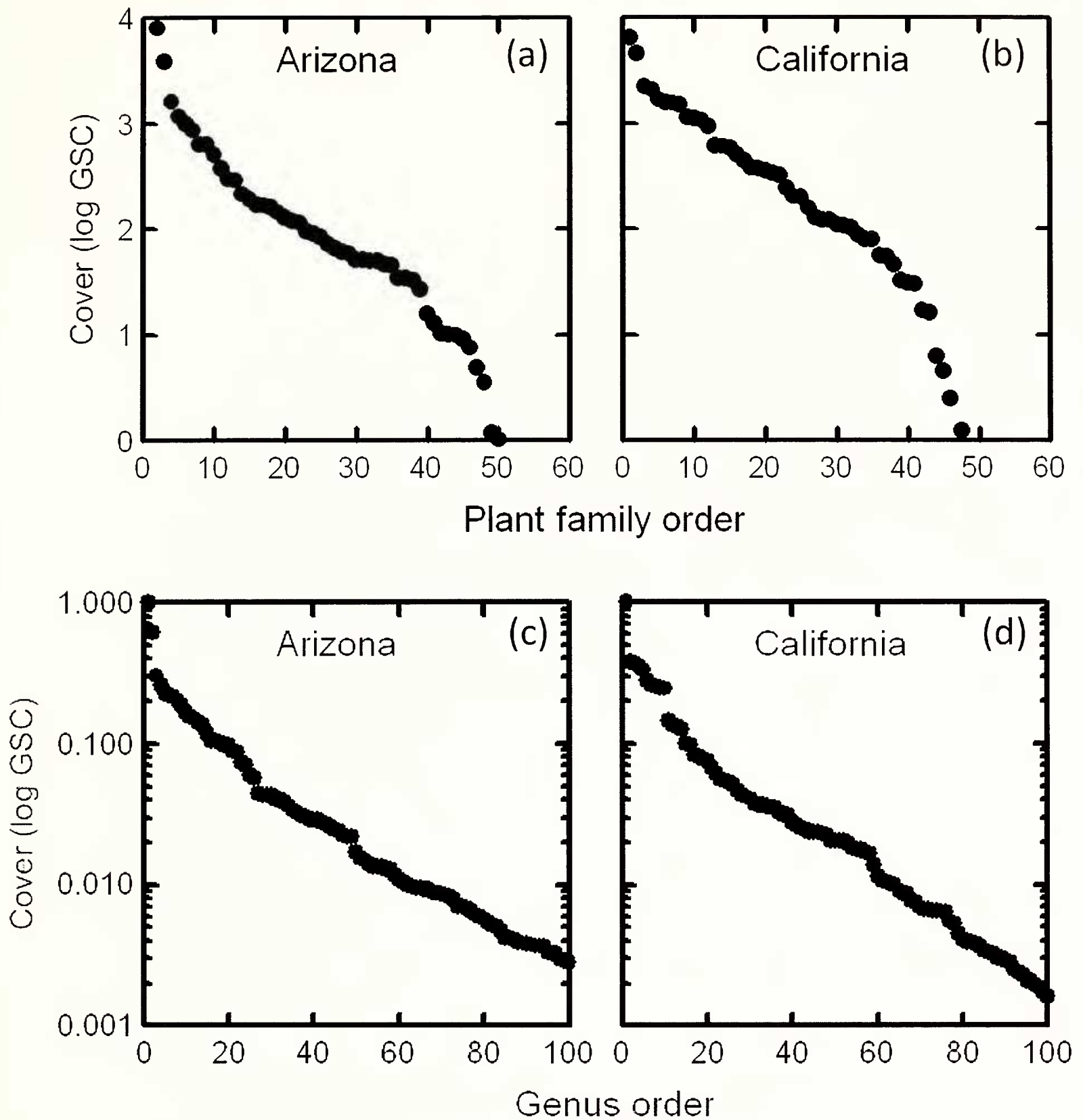


FIG. 2. Rank order distribution of (a, b) plant families and (c, d) genera in Arizona and California. GSC is ground surface cover.

Field Methods

In Arizona, there were two growing seasons following both the summer rains and the winter rains so sampling was first done in fall 2002 and then again in spring 2003, and this sampling regime was repeated for a second year. In the winter-rainfall chaparral of California sampling was conducted only in spring of 2004 and 2005. Each site consisted of a 20 m \times 50 m sample plot, positioned parallel to the slope contour, which is considered appropriate for capturing the greatest variation in community composition (Keeley and Fotheringham 2005). Each of these tenth hectare sites were subdivided into 10 nested 100 m²

square subplots, each with a single nested 1 m² square quadrat in an outside corner. Cover and density were recorded for each species within the quadrats, and a list of additional species was recorded from the surrounding subplot. Cover was visually estimated and a percentage of ground surface covered was recorded for each species. Density was recorded for each species with counts where density was less than approximately 25 individuals per quadrat, and with estimates at higher densities. Seedlings and resprouts of the same species were counted and recorded separately. Vouchers were collected for all specimens and have been deposited in the herbarium in J. Keeley's laboratory. All plant

TABLE 2. TOP 75 NATIVE GENERA IN THE ARIZONA AND CALIFORNIA POSTFIRE SITES BASED ON AERIAL COVERAGE.

Arizona	Normalized cover	Arizona	Normalized cover
<i>Eragrostis</i>	1.000	<i>Amaranthus</i>	0.029
<i>Dalea</i>	0.609	<i>Portulaca</i>	0.029
<i>Glandularia</i>	0.301	<i>Bothriochloa</i>	0.029
<i>Bouteloua</i>	0.258	<i>Plagiobothrys</i>	0.028
<i>Bidens</i>	0.227	<i>Arctostaphylos</i>	0.027
<i>Quercus</i>	0.218	<i>Schinus</i>	0.026
<i>Muhlenbergia</i>	0.217	<i>Cryptantha</i>	0.024
<i>Lotus</i>	0.200	<i>Juniperus</i>	0.024
<i>Mollugo</i>	0.187	<i>Marina</i>	0.022
<i>Heterosperma</i>	0.166	<i>Gnaphalium</i>	0.022
<i>Mimosa</i>	0.154	<i>Boerhavia</i>	0.022
<i>Chamaecrista</i>	0.150	<i>Phaseolus</i>	0.017
<i>Melampodium</i>	0.142	<i>Chamaesyce</i>	0.016
<i>Urochloa</i>	0.136	<i>Yucca</i>	0.015
<i>Nolina</i>	0.117	<i>Cyperus</i>	0.014
<i>Aristida</i>	0.105	<i>Digitaria</i>	0.013
<i>Desmodium</i>	0.104	<i>Aeschynomene</i>	0.013
<i>Ipomoea</i>	0.102	<i>Anoda</i>	0.013
<i>Helimeris</i>	0.098	<i>Opuntia</i>	0.013
<i>Panicum</i>	0.097	<i>Descurainia</i>	0.013
<i>Calliandra</i>	0.089	<i>Drymaria</i>	0.012
<i>Leptochloa</i>	0.088	<i>Eriogonum</i>	0.011
<i>Acalypha</i>	0.073	<i>Gymnosperma</i>	0.010
<i>Erodium</i>	0.070	<i>Commelina</i>	0.010
<i>Evolvulus</i>	0.060	<i>Dyssodia</i>	0.010
<i>Sida</i>	0.056	<i>Triticum</i>	0.010
<i>Sphaeralcea</i>	0.044	<i>Diodia</i>	0.009
<i>Lycurus</i>	0.043	<i>Gilia</i>	0.009
<i>Astragalus</i>	0.043	<i>Scleropogon</i>	0.009
<i>Schizachyrium</i>	0.043	<i>Garrya</i>	0.009
<i>Elionurus</i>	0.040	<i>Sanvitalia</i>	0.009
<i>Ceanothus</i>	0.040	<i>Linum</i>	0.009
<i>Crotalaria</i>	0.038	<i>Trachypogon</i>	0.008
<i>Krameria</i>	0.036	<i>Agave</i>	0.008
<i>Cathastecum</i>	0.034	<i>Hackelochloa</i>	0.008
<i>Prosopis</i>	0.033	<i>Erigeron</i>	0.007
<i>Dasyhiron</i>	0.031	<i>Salvia</i>	0.007
<i>Chenopodium</i>	0.030		
California	Normalized cover	California	Normalized cover
<i>Adenostoma</i>	1.000	<i>Allophylhum</i>	0.026
<i>Phacelia</i>	0.379	<i>Solanum</i>	0.025
<i>Calystegia</i>	0.364	<i>Silene</i>	0.025
<i>Arctostaphylos</i>	0.354	<i>Cercocarpus</i>	0.023
<i>Lotus</i>	0.331	<i>Malacothammus</i>	0.023
<i>Ceanothus</i>	0.280	<i>Styrax</i>	0.023
<i>Helianthemum</i>	0.261	<i>Navarretia</i>	0.023
<i>Cryptantha</i>	0.256	<i>Hypochoeris</i>	0.022
<i>Quercus</i>	0.248	<i>Garrya</i>	0.020
<i>Emmenanthe</i>	0.245	<i>Gastrium</i>	0.020
<i>Calochortus</i>	0.145	<i>Calyptidium</i>	0.019
<i>Eriodictyon</i>	0.135	<i>Mimulus</i>	0.018
<i>Xylococcus</i>	0.131	<i>Erodium</i>	0.018
<i>Chlorogalum</i>	0.100	<i>Lepechinia</i>	0.017
<i>Antirrhinum</i>	0.098	<i>Helianthus</i>	0.017
<i>Marah</i>	0.082	<i>Nassella</i>	0.012
<i>Rhamnus</i>	0.081	<i>Penstemon</i>	0.011
<i>Chaenactis</i>	0.077	<i>Lupinus</i>	0.010
<i>Camissonia</i>	0.075	<i>Galium</i>	0.010
<i>Dicentra</i>	0.068	<i>Monardella</i>	0.010
<i>Dendromecon</i>	0.061	<i>Lomatium</i>	0.009
<i>Malosma</i>	0.055	<i>Erigeron</i>	0.009
<i>Salvia</i>	0.055	<i>Fremontodendron</i>	0.009

TABLE 2. CONTINUED.

California	Normalized cover	California	Normalized cover
<i>Dichelostemma</i>	0.053	<i>Daucus</i>	0.008
<i>Cneoridium</i>	0.051	<i>Melica</i>	0.007
<i>Chamaebatia</i>	0.046	<i>Papaver</i>	0.007
<i>Eriophyllum</i>	0.042	<i>Cupressus</i>	0.007
<i>Zigadenus</i>	0.042	<i>Selaginella</i>	0.007
<i>Pickeringia</i>	0.041	<i>Elymus</i>	0.007
<i>Nemocladus</i>	0.037	<i>Muilla</i>	0.007
<i>Gilia</i>	0.037	<i>Apistrum</i>	0.007
<i>Yucca</i>	0.036	<i>Ribes</i>	0.006
<i>Pterostegia</i>	0.036	<i>Eriogonum</i>	0.006
<i>Brassica</i>	0.035	<i>Lonicera</i>	0.005
<i>Hazardia</i>	0.035	<i>Claytonia</i>	0.005
<i>Filago</i>	0.033	<i>Chorizanthe</i>	0.004
<i>Rhus</i>	0.031	<i>Pellaea</i>	0.004
<i>Trichostema</i>	0.031	<i>Leymus</i>	0.004
<i>Mentzelia</i>	0.028		

nomenclature follows Hickman (1993) for California and USDA (2009) for Arizona.

Precipitation data for Arizona were obtained from <http://cdo.ncdc.noaa.gov/CDO/> data product (accessed May 2008) for climate stations nearest to the study sites. Precipitation data for California were obtained from the Western Regional Climate Center (<http://www.wrcc.dri.edu/summary/Climsmsca.html>; accessed April 2007). Average precipitation for the sites in Arizona and California were comparable (Fig. 1a). Both regions have significant winter rains followed by a late spring and early summer drought. In California drought continues until late fall whereas Arizona has summer rains that begin in July and extend through September. A substantial proportion of total rain occurs during the 'summer' (July, August and September) in Arizona in contrast to California (Fig. 1b).

Data Analysis

Statistical comparisons and regressions were calculated and displayed graphically with Systat 11.0 (Richmond, CA, USA). Comparisons between Arizona and California were made with a two-tailed t-test for all quantitative parameters.

Compositional differences between sites within a region and between regions were evaluated using Jaccard's similarity coefficient, which provides a measure of similarity between two sets of data. This coefficient was calculated using a modified form of Jaccard's index (see Table 10.2 in Mueller-Dombois and Ellenberg 1974), based on presence/absence as:

$$JI_{cov} = \frac{MC}{MA + MB} \times 100$$

where MC is the number of taxa present in both regions, MA is number of taxa present only in Arizona and MB is for taxa present only in

California, and the coefficient expressed as a percentage. The value ranges from 0%, where the two data sets share no taxa, to 100% with complete overlap in taxa. This index was calculated for all plant families and all genera shared between sites within a region and between regions, i.e., for all pairwise comparisons of sites within Arizona, and within California and then for all comparisons between Arizona sites and California sites. The non-parametric Wilcoxon signed ranks test was used to compare the Jaccard's indices calculated within Arizona to those calculated between Arizona and California sites to determine if Arizona sites were more similar to one another than they were to California.

RESULTS

Taxonomic Patterns

Between the Arizona and California sites there were 44 plant families in common and an additional 19 families recorded just at the Arizona sites and nine just at the California sites (Appendix 1). Based on total cover over the two years of study in both Arizona and California, the top 15 families were quite different (Table 1). Although about half of the top 15 families were shared between both regions, the most dominant families were different. In Arizona the top two families were the Poaceae and Fabaceae whereas in California it was the Hydrophyllaceae and Rosaceae. Families were generally more evenly distributed in California than in Arizona, as illustrated by the observation that the top 15 families were present in sites at all fires in California, whereas in Arizona only the top 10 families were represented at all fires.

A similar difference between regions is illustrated by the pattern of equitability in rank order distribution of families (Fig. 2a, b). In Arizona

TABLE 3. SPECIES FOUND IN BOTH THE ARIZONA AND CALIFORNIA STUDY SITES. This is not meant to suggest these are the only species found in chaparral of the two regions but just what was recorded from our 40 study sites in Arizona and 250 sites in California.

Annuals

<i>Allophyllum gilioides</i> (Benth). A. D. Grant & V. E. Grant	Polemoniaceae
<i>Aristida adscensionis</i> L.	Poaceae
<i>Bowlesia incana</i> Ruiz & Pav.	Apiaceae
<i>Chenopodium berlandieri</i> Moq.	Chenopodiaceae
<i>Calandrinia ciliata</i> (Ruiz & Pav.) DC.	Portulacaceae
<i>Conyza canadensis</i> (L.) Cronquist	Asteraceae
<i>Cryptantha micrantha</i> (Torr.) I. M. Johnst.	Boraginaceae
<i>Cryptantha muricata</i> (Hook & Arn.) A. Nelson & J. F. Macbr.	Boraginaceae
<i>Daucus pusillus</i> Michx.	Apiaceae
<i>Eriastrum sapphirinum</i> (Eastw.) H. Mason	Polemoniaceae
<i>Galium aparine</i> L.	Rubiaceae
<i>Gilia leptantha</i> Parish	Polemoniaceae
<i>Lepidium virginicum</i> L.	Brassicaceae
<i>Lotus humistratus</i> Greene	Fabaceae
<i>Lupinus concinnus</i> J. Agardh	Fabaceae
<i>Lupinus sparsiflorus</i> Benth.	Fabaceae
<i>Malacothrix clevelandii</i> A. Gray	Asteraceae
<i>Pectocarya setosa</i> A. Gray	Boraginaceae
<i>Phacelia distans</i> Benth.	Hydrophyllaceae
<i>Phlox gracilis</i> (Hook.) Greene	Polemoniaceae
<i>Rafinesquia californica</i> Nutt.	Asteraceae
<i>Silene antirrhina</i> L.	Caryophyllaceae
<i>Stephanomeria exigua</i> Nutt.	Asteraceae
<i>Stellaria nitens</i> Nutt.	Caryophyllaceae
<i>Stylocline gnaphalioides</i> Nutt.	Asteraceae
<i>Thysanocarpus curvipes</i> Hook.	Brassicaceae
<i>Triodanis biflora</i> (Ruiz & Pav.) Greene	Campanulaceae
<i>Triodanis perfoliata</i> (L.) Nieuwl.	Campanulaceae
<i>Vulpia microstachys</i> (Nutt.) Munro	Poaceae
<i>Vulpia octoflora</i> (Walter) Rydb.	Poaceae
<i>Yabea microcarpa</i> (Hook. & Arn.) Koso-Pol.	Apiaceae
Herbaceous perennials	
<i>Aristida purpurea</i> Nutt.	Poaceae
<i>Astragalus trichopodus</i> (Nutt.) A. Gray	Fabaceae
<i>Bothriochloa barbinodis</i> (Lag.) Herter	Poaceae
<i>Datura wrightii</i> Regel	Solanaceae
<i>Dichelostemma capitatum</i> (Benth.) Alph. Wood	Amaryllidaceae
<i>Gnaphalium bicolor</i> Anderb.	Asteraceae
<i>Gnaphalium canescens</i> DC.	Asteraceae
Subshrubs or suffrutescents	
<i>Atriplex semibaccata</i> R. Br.	Chenopodiaceae
<i>Brickellia californica</i> (Torr. & A. Gray) A. Gray	Asteraceae
<i>Encelia farinosa</i> A. Gray ex Torr.	Asteraceae
<i>Eriogonum wrightii</i> Torr. ex Benth.	Polygonaceae
<i>Gutierrezia sarothrae</i> (Pursh) Britton & Rusby	Asteraceae
<i>Porophyllum gracile</i> Benth.	Asteraceae
<i>Rhus trilobata</i> Nutt.	Anacardiaceae
<i>Senecio flaccidus</i> Less.	Asteraceae
<i>Solanum douglasii</i> Dunal	Solanaceae
<i>Yucca schidigera</i> Roezl ex Ortgies	Liliaceae
Shrubs	
<i>Arctostaphylos pungens</i> Kunth	Ericaceae
<i>Artemisia tridentata</i> Nutt.	Asteraceae
<i>Baccharis salicifolia</i> (Ruiz & Pav.) Pers.	Asteraceae
<i>Ceanothus greggii</i> A. Gray	Rhamnaceae
<i>Garrya wrightii</i> Torr.	Garryaceae
<i>Rhamnus crocea</i> Nutt.	Rhamnaceae
<i>Sambucus mexicana</i> C. Presl. ex DC.	Caprifoliaceae

TABLE 3. CONTINUED.

Annual species alien to Arizona and California

<i>Ambrosia artemisiifolia</i> L.	Asteraceae
<i>Brassica nigra</i> (L.) W. D. J. Koch	Brassicaceae
<i>Bromus madritensis</i> L.	Poaceae
<i>Bromus tectorum</i> L.	Poaceae
<i>Chenopodium album</i> L.	Chenopodiaceae
<i>Erodium cicutarium</i> (L.) L'Hér. ex Aiton	Geraniaceae
<i>Lactuca serriola</i> L.	Asteraceae
<i>Marrubium vulgare</i> L.	Lamiaceae
<i>Phalaris minor</i> Retz.	Poaceae
<i>Poa annua</i> L.	Poaceae
<i>Schismus barbatus</i> (L.) Thell.	Poaceae
<i>Sisymbrium altissimum</i> L.	Brassicaceae
<i>Sisymbrium irio</i> L.	Brassicaceae
<i>Salsola tragus</i> L.	Chenopodiaceae
<i>Sonchus tenerrimus</i> L.	Asteraceae
<i>Vulpia bromoides</i> (L.) A. Gray	Poaceae

there was a much larger difference between the top few families and the remaining families, whereas in California cover was somewhat more equally distributed among families. For example two orders of magnitude cover below the top family in Arizona comprised only about 20 families, whereas in California it was almost double that number.

Unlike the family distribution, where the majority were in common between regions, many fewer genera were common between regions than were unique to one or the other region (Appendix 2). There were only 109 genera recorded from sites in both regions, but there were 148 genera recorded just in Arizona sites and 78 recorded just in California sites. Based on cover, of the top 75 genera in Arizona, only 16 were also in the top 75 in California and of the top 75 in California only 22 were in the top group in Arizona (Table 2). Genera important in both regions (defined as in the top 75) include the shrubs *Arctostaphylos*, *Ceanothus*, *Garrya*, and *Quercus*, subshrubs *Baccharis*, *Eriogonum*, *Salvia*, and *Yucca*, and suffrutescents *Erigeron* and *Lotus* (Table 2). The cover distribution for the top genera (Fig. 2c, d) followed similar curves in Arizona and California, indicating greater equitability in both regions than observed with families.

In Arizona there were substantially more species recorded from the 40 study sites (577) than for the 250 sites in California (439) despite covering a roughly similar-sized geographical area. However, in Arizona this covered an east-west gradient and in California a north-south gradient.

As a general rule none of the dominant herbaceous species in Arizona chaparral were present or well represented in California chaparral, and vice versa. One of the most conspicuous and widespread postfire species in Arizona

was the fall germinating ephemeral herbaceous perennial *Verbena bipinnatifida* Nutt. (= *Glandularia b.*), a species not found in the California postfire chaparral. In California the most conspicuous postfire ephemerals were Hydrophyllaceae, most of which were absent or of very minor importance in Arizona chaparral.

However, there were more than 30 minor species in common between both regions (Table 3); e.g., *Allophyllum gilioides* A.D. Grant & V.E. Grant, *Calandrinia ciliate* (Ruiz & Pav.) DC., *Lupinus sparsiflorus* Benth., *Malacothrix clevelandii* A. Gray, and *Rafinesquia californica* Nutt., all of which are spring annuals. Of the herbaceous perennials the one that stands out as being very common in both regions was *Dichelostemma capitatum* (Benth.) Alph. Most of the subshrubs listed were widespread but never locally common. Several shrubs were widespread in both regions, in particular *Arctostaphylos pungens* Kunth, *Ceanothus greggii* A. Gray and *Rhamnus crocea* Nutt. More than 15 alien species were common between both regions, and all were annuals (Table 3).

The main shrub species in Arizona were seedlings of the obligate seeders *Arctostaphylos pungens*, *Ceanothus greggii* and *C. fendleri* A. Gray and resprouts of *Quercus turbinella* Greene, *Rhus trilobata* Nutt., and *Baccharis salicifolia* (Ruiz & Pav.) Pers. Postfire sites in California were dominated by resprouts and seedlings of *Adenostoma fasciculatum* Hook. & Arn, *Arctostaphylos* spp., and *Ceanothus* spp. as well as resprouts of *Quercus berberidifolia* Liebm. Subshrubs and other less woody and shorter-lived suffrutescents were very different between these regions. In Arizona the genus *Dalea* was very important as well as *Krameria erecta* Willd. ex Schult. and species of *Senecio* and *Solanum*, but this niche was filled largely by *Lotus scoparius* (Nutt.) Ottley, *Helianthemum scoparium* Nutt.

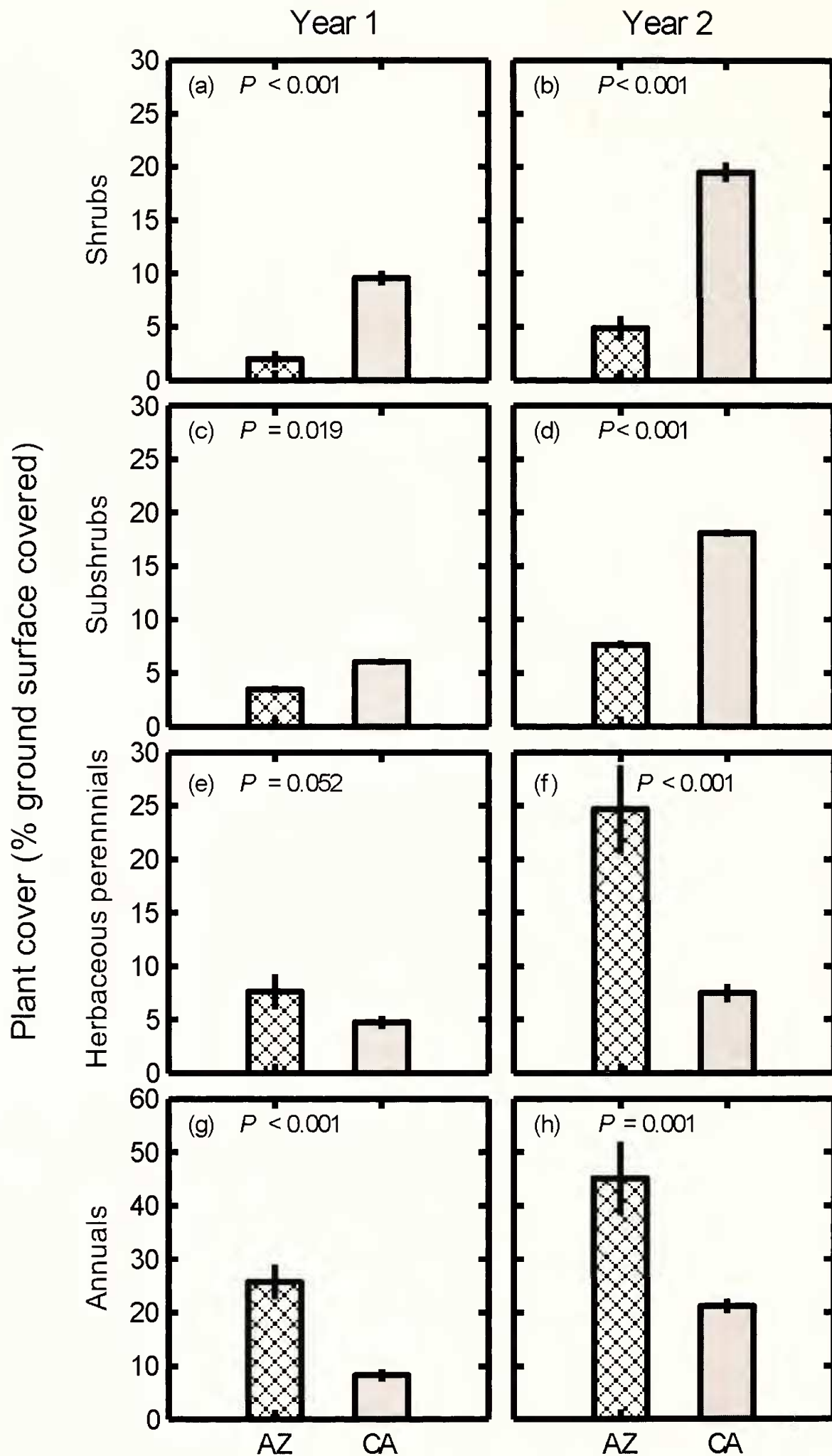


FIG. 3. Plant cover in spring of year 1 and year 2 presented by life form (AZ = Arizona, CA = California, subshrub category includes the weakly woody suffrutescents). Error bars are the standard error of the mean. Note the scale for annuals is double that for other life forms.

and *Calystegia macrostegia* (Greene) Brummitt in California. Herbaceous floras were very different between the two regions with Poaceae dominating in Arizona and Hydrophyllaceae in California.

Postfire Changes in Cover and Diversity

Total cover was around 20% in the first postfire year and not significantly different

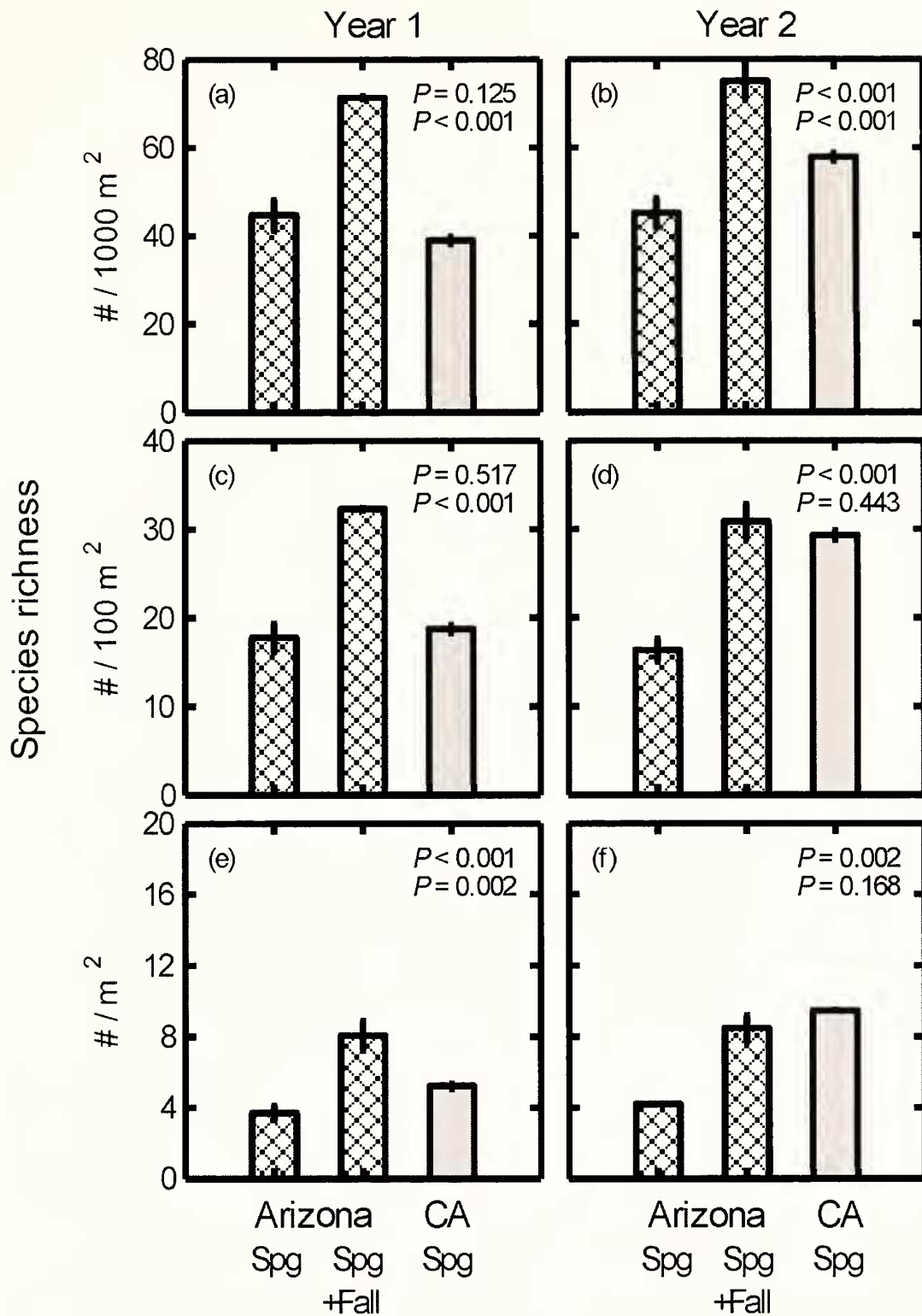


FIG. 4. Species diversity (including native and non-native species) for the spring flora and total flora in Arizona and spring flora in California at three scales in both years (Arizona, CA = California, Spg = spring). Two-tailed t-test for (top P-value) Arizona spring vs. California spring and (bottom P-value) Arizona total vs. California spring. Error bars are the standard error of the mean.

between Arizona and California, but in the second year cover more than doubled in California and was significantly greater than in Arizona ($P < 0.001$). These two regions differed markedly in the importance of different growth forms. Shrub cover was about five times greater in California than in Arizona in the first two postfire years (Fig. 3a, b), and subshrubs also had significantly greater cover in California (Fig. 3c, d). In contrast, herbaceous species, both perennials (Fig. 3e, f) and annuals (Fig. 3g, h) had significantly more cover in Arizona than in California. By the second postfire year herbaceous perennials, mostly grasses, had about four times more cover in Arizona and annuals had about twice as much as California. In short,

postfire cover in California was more or less equally distributed among different growth forms than in Arizona.

Species richness in the first spring after fire was slightly higher in California at the 1 m² scale (Fig. 4e), but not significantly different at larger scales (Fig. 4c, a). However, this does not capture the full annual diversity in Arizona due to the double growing seasons resulting from a bimodal rainfall pattern. As a consequence Arizona produced two different herbaceous floras, one in fall and one in spring. The total first year diversity (fall 2002 plus spring 2003 in Arizona vs. just the spring 2003 flora in California) was significantly higher in Arizona at all scales (Fig. 4a, c, e).

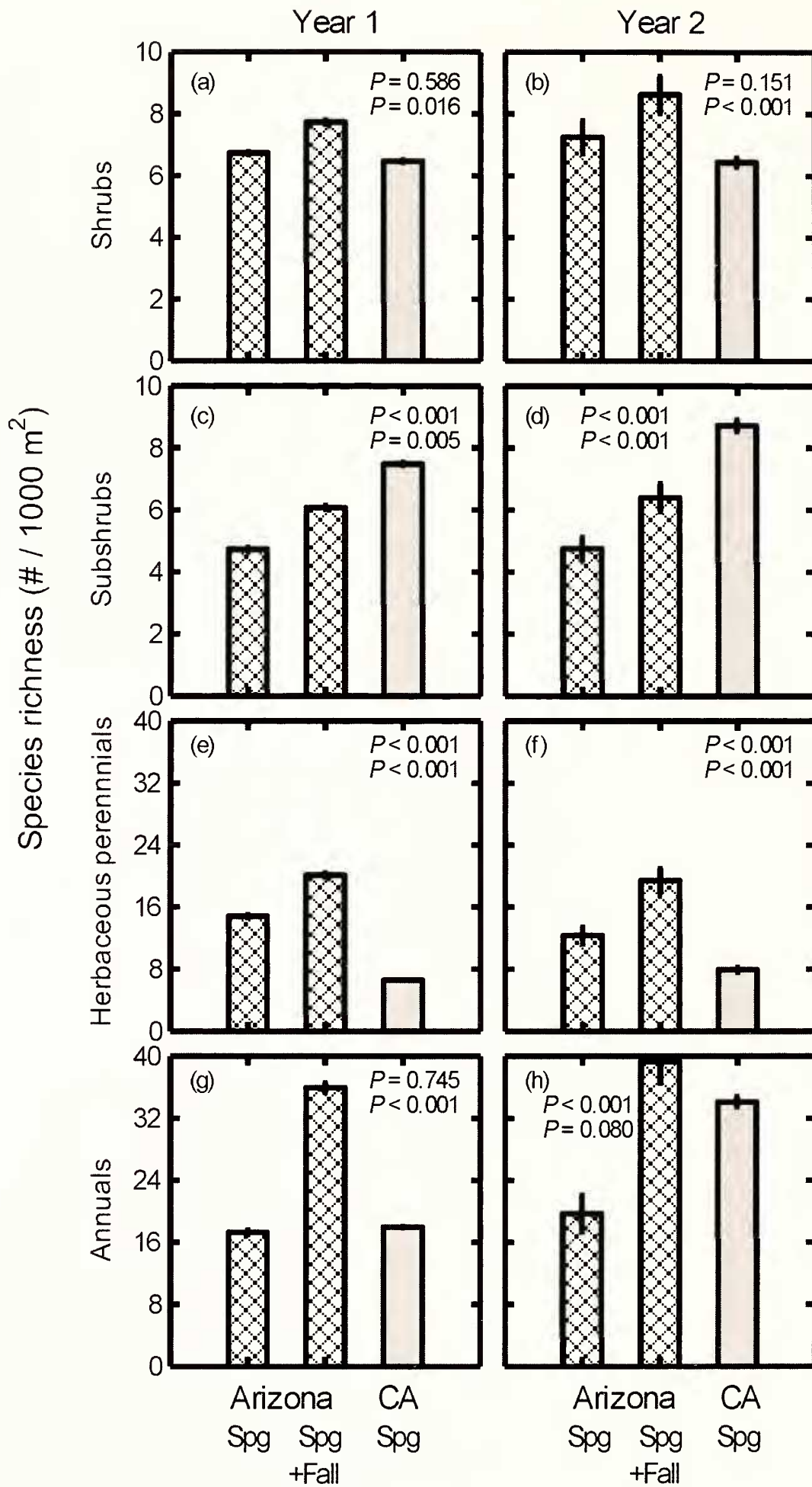


FIG. 5. Species diversity at the site level (tenth ha) for the spring flora and total flora in Arizona and spring flora in California in both years presented by life form (Arizona, CA = California, Spg = spring). Two-tailed t-test for (top P-value) Arizona spring vs. California spring and (bottom P-value) Arizona total vs. California spring. Error bars are the standard error of the mean.

In the second postfire spring, diversity rose at all scales in California but not in Arizona so spring floras were significantly more diverse in California at all scales (Fig. 4b, d, f). Total second year diversity was significantly greater in Arizona at the largest spatial scale (Fig. 4b).

The contribution of different growth forms to diversity at the site level (tenth ha) differed between regions. In the first spring following fire, woody plant diversity was similar between both regions (Fig. 5a), but when the fall flora in Arizona was added in the total for the year was

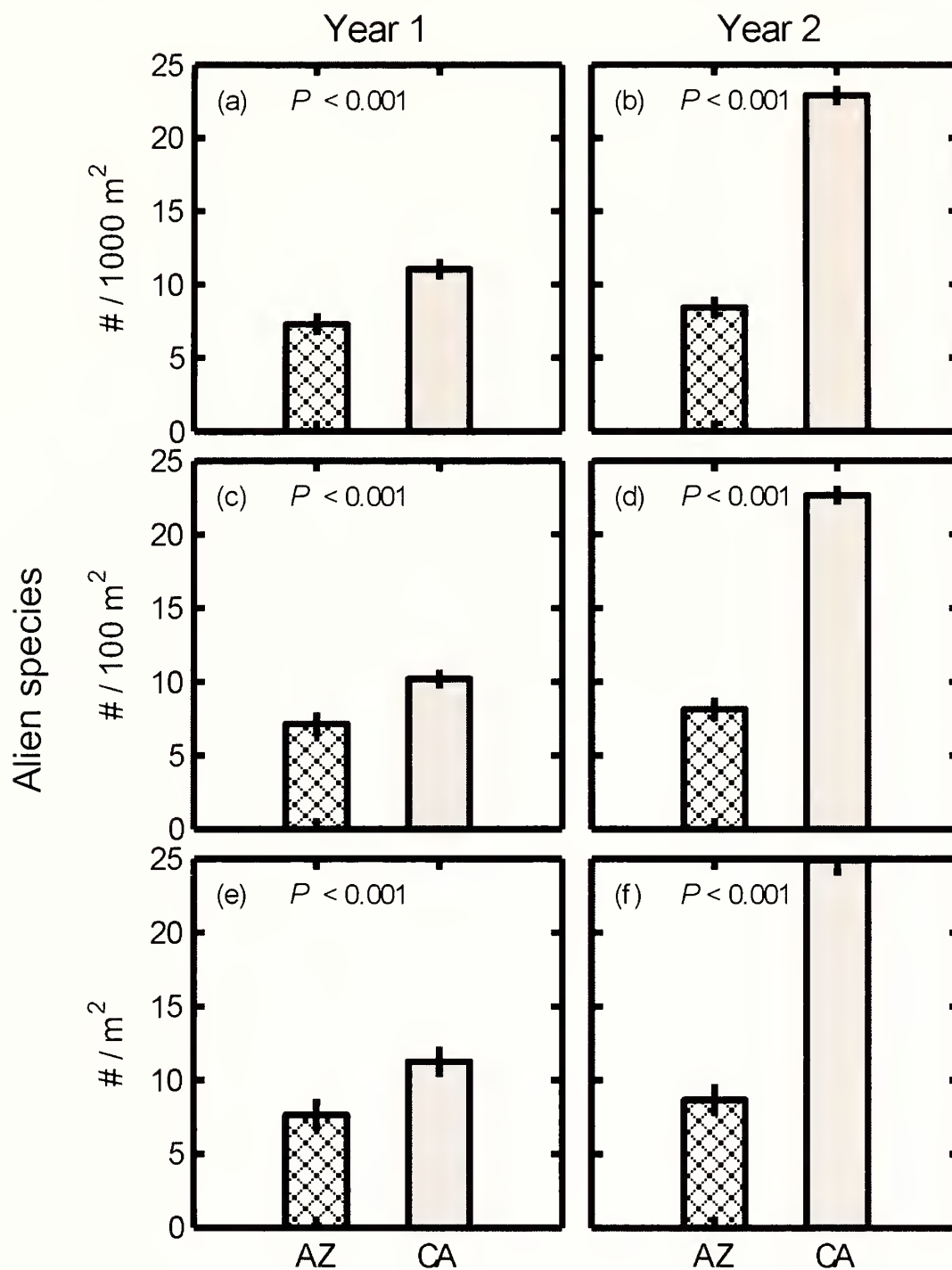


FIG. 6. Alien species diversity at three scales for the annual total (combined fall and spring for Arizona and spring for California in year 1 and year 2 (AZ = Arizona, CA = California)). Error bars are the standard error of the mean. Note scale remains the same in all panels.

slightly greater in Arizona (Fig. 5a). Subshrub (including suffrutescents) diversity was greater in California than either the spring or spring plus fall total in Arizona (Fig. 5c). However, herbaceous perennial diversity was greater in Arizona in the spring and even greater when fall diversity was added in (Fig. 5e). Spring annual diversity was similar in both regions (Fig. 5g) but when the fall flora in Arizona was added in (Fig. 5g) diversity of annuals was substantially greater in Arizona. These patterns remained the same in the second year (Fig. 5b, d, f, h).

Alien plant cover comprised only a few percent of the total cover in the first year (measured in spring) and was not significantly different between Arizona and California ($P = 0.486$). However, by spring of the second year, total cover of aliens in California had increased about 5-fold and was significantly greater than in Arizona ($P = 0.002$). Species diversity of aliens

was significantly higher at all spatial scales in California in both years (Fig. 6). In the second year alien species comprised 8% of the Arizona flora and 22% of the California flora.

Community Similarity

Jaccard's index was used to compare the compositional similarity within regions and between regions. Since few species were important in both Arizona and California the focus was on plant families and genera. Sites were grouped by the six fires in Arizona and the four fires in California and comparisons were made on first year floras. Comparisons of Arizona sites vs. other Arizona sites, and Arizona sites vs. California sites were made for fall and spring. In California, there was only one growing season in the spring, so comparisons of fall families or fall genera in Arizona were made against spring floras in California.

TABLE 4. PERCENTAGE SIMILARITY BETWEEN BURNS USING PRESENCE/ABSENCE JACCARD'S INDEX. Arizona sites are presented from west to east and California sites from north to south. *In California, there was only one growing season in the spring, so comparisons of fall taxa in Arizona were made against spring taxa in California.

	AZ - Bullock	AZ - Upper Bullock	AZ - Merritt/ Ryan	AZ - Darnel	AZ - Walnut	CA - Grand Prix/Old	CA - Paradise	CA - Cedar	CA - Otay
Families									
<i>Fall Az - Spring CA*</i>									
AZ - Oracle	73	44	53	55	56	48	40	46	45
AZ - Bullock		45	55	60	61	43	39	44	40
AZ - Upper Bullock			47	44	42	33	33	34	36
AZ - Merritt/Ryan				68	60	37	32	35	37
AZ - Darnel					67	40	38	43	38
AZ - Walnut						39	42	44	41
<i>Spring in AZ & CA</i>									
AZ - Oracle	78	42	46	56	62	55	50	58	58
AZ - Bullock		48	48	58	67	57	49	59	60
AZ - Upper Bullock			49	44	35	36	36	37	42
AZ - Merritt/Ryan				57	44	29	31	35	33
AZ - Darnel					60	40	38	43	37
AZ - Walnut						40	38	43	37
CA - Grand Prix/Old							70	67	76
CA - Paradise								80	79
CA - Cedar									82
Genera									
<i>Fall Az - Spring CA*</i>									
AZ - Oracle	54	28	31	37	37	14	9	13	10
AZ - Bullock		31	41	31	46	11	10	10	9
AZ - Upper Bullock			26	31	30	9	6	6	6
AZ - Merritt/Ryan				43	45	9	6	7	7
AZ - Darnel					49	8	7	7	5
AZ - Walnut						10	9	10	8
<i>Spring in AZ & CA</i>									
AZ - Oracle	54	33	31	28	42	17	14	17	15
AZ - Bullock		33	33	30	45	18	12	15	13
AZ - Upper Bullock			30	23	26	14	13	13	13
AZ - Merritt/Ryan				30	36	8	8	8	7
AZ - Darnel					42	8	6	7	5
AZ - Walnut						16	14	15	14
CA - Grand Prix/Old							49	49	54
CA - Paradise								63	54
CA - Cedar									61

Based on presence/absence the Jaccard's index for families and genera in fall and spring (Table 4) generally showed that intraregional comparisons of fires (AZ fires vs. AZ fires or CA fires vs. CA fires) were more similar than comparisons between regions (AZ vs. AZCA or CA vs. AZCA).

In Arizona the two western most sites (Oracle and Bullock) were markedly similar in families and genera but that changed with elevation (Upper Bullock) and in comparison with the eastern most sites (Table 4). In California, sites were much more similar to each other than

observed within Arizona sites, despite being distributed across a similar-sized area.

For both families and genera the spring flora in Arizona was much more similar to California's spring flora than was the fall flora in Arizona. In addition, the western most sites in Arizona (Oracle and Bullock) were more similar to California than the eastern most sites (Darnel and Walnut).

To summarize these patterns the average Jaccard's index is presented for all Arizona site comparisons, for all California site comparisons and for all comparisons of Arizona and California sites

TABLE 5. COMPOSITIONAL SIMILARITY BETWEEN BURNED AREAS USING JACCARD'S INDEX BASED ON PRESENCE/ABSENCE FOR PLANT FAMILIES AND GENERA IN THE FALL AND SPRING, BASED ON DATA IN TABLE 4. AZ = average of all pairwise comparisons of Arizona sites grouped by fire, CA = average of all pairwise comparisons of California sites grouped by fire, AZCA = all pairwise comparisons of Arizona vs. California sites grouped by fire). *In California, there was only one growing season in the spring, so comparisons of fall taxa in Arizona were made against spring taxa in California.

	Average Jaccard's percentage similarity			P-value for Wilcoxon signed ranks test		
	AZ	AZCA	CA	AZ vs. CA	AZ vs. AZCA	CA vs. AZCA
Families						
Fall*	55	39	–	0.046	<0.001	–
Spring	53	46	75	0.046	0.069	0.028
Genera						
Fall*	39	9	–	0.046	<0.001	–
Spring	34	12	55	0.046	<0.001	0.028

(Table 5). Based on these averages it is apparent, at both the family and genus level, California sites were significantly more similar to one another than were Arizona sites. The average for regional comparisons between Arizona and California was much lower for families and markedly lower for genera than that index calculated within each region.

Aliens were not well represented in many Arizona sites and this likely contributed to the fact that at the level of both families and genera, similarity between sites was much less (Table 6) than for the flora as a whole (Table 5). This stands in contrast to the California sites where alien families and genera were quite similar between sites (Table 6). The average similarity within Arizona sites was not significantly different than the similarity index between Arizona and California sites, whereas California sites had a significantly higher index than that calculated between California and Arizona.

DISCUSSION

California chaparral occurs under a winter rain – summer drought climate in contrast to the

bimodal rainfall pattern characteristic of Arizona chaparral. Although both have winter rains, California sites typically have higher winter rainfall than Arizona sites (40–60% of the annual total in California vs 20–30% in Arizona). These rainfall patterns contribute to differences in fire seasons; Arizona commonly has late spring – early summer fires and the California fire season is largely in the late summer and fall (Keeley 2000), although earlier in years with dry winters (Dennison et al. 2008).

In addition to occurring under a different climatic regime, Arizona chaparral tends to be distributed at higher elevations than in California sites, apparently because precipitation regimes conducive to chaparral occur at higher elevations in Arizona than in California (Mooney and Miller 1985). This likely accounts for why the ubiquitous Californian chaparral shrub *Adenostoma fasciculatum* is missing from Arizona; in California it drops out of interior sites with cold winters (Keeley and Davis 2007).

Arizona and California chaparral communities share many of the same dominant woody species, including species of *Arctostaphylos*, *Baccharis*, *Ceanothus*, *Cercocarpus*, *Eriogonum*, *Garrya*,

TABLE 6. ALIEN PLANT SIMILARITY BETWEEN BURNED AREAS USING JACCARD'S INDEX BASED ON PRESENCE/ABSENCE FOR PLANT FAMILIES AND GENERA IN THE FALL AND SPRING, BASED ON SIMILAR COMPARISONS AS SHOWN IN TABLE 4. AZ = average of all pairwise comparisons of Arizona sites grouped by fire, CA = average of all pairwise comparisons of California sites grouped by fire, AZCA = all pairwise comparisons of Arizona vs. California sites grouped by fire. *In California, there was only one growing season in the spring, so comparisons of fall taxa in Arizona were made against spring taxa in California.

	Average Jaccard's percentage similarity			P-value for Wilcoxon signed ranks test		
	AZ	AZCA	CA	AZ vs. CA	AZ vs. AZCA	CA vs. AZCA
Families						
Fall*	27	33	–	0.028	0.331	–
Spring	26	26	75	0.028	0.950	0.028
Genera						
Fall*	20	6	–	0.046	<0.001	–
Spring	19	12	59	0.028	0.022	0.028

Quercus, *Rhamnus*, *Rhus*, and *Salvia*. In both regions these dominants exhibit similar patterns of postfire recovery including resprouting and seedling recruitment from soil-stored seed banks. Following summer wildfires Arizona chaparral recovers very rapidly in concert with the summer rains that begin usually in July. All resprouting woody species initiate resprouts during this rainy season. In California, resprouting species may begin regrowth soon after fires but this appears to be dependent on soil moisture as it is commonly observed that resprouting in dry years it is delayed until the winter rainy season (Keeley 2000).

The phenology of seedling recruitment in *Ceanothus* and *Arctostaphylos* shrub species is remarkably similar in that it occurs towards the end of the winter rainy season in both regions. Thus, the winter rainfall is one climatic characteristic that links these regions in terms of some functional type responses. Another is the spring postfire annual-dominated flora in both regions.

However, the ephemeral postfire floras exhibit a number of differences between regions. Most noteworthy is the dual postfire floras in Arizona. Not only do fall and spring rains result in two growing seasons but different floras are produced in fall and spring. The spring flora in Arizona bears a strong systematic resemblance to California whereas the fall flora is quite distinct and has elements that have a more neotropical affinity (Fotheringham 2009). As a consequence, the total yearly diversity is substantially higher in Arizona than in California from small to large scales (Fig. 4). At the community level (1000 m²) species richness in Arizona is comparable to some of the most species rich communities known from temperate latitudes (Keeley and Fotheringham 2003).

Another prominent difference between these climatically different regions is the greater importance of herbaceous perennials in the Arizona chaparral. This is likely tied to the differences in summer drought between the two regions. In California the drought, on average, lasts from late spring to early fall and places a severe stress on survival of perennials, particularly herbaceous perennials. In Arizona the drought is cut short by summer rains and this works to favor survival of herbaceous perennials. One of the most striking differences in the postfire floras between these two regions is the prominence of Poaceae in Arizona, in particular the very diverse and dominant C₄ bunchgrass flora. The importance of C₄ bunchgrasses is to be expected in this summer rain climate and their near total absence in California is consistent with what is known about the distribution of C₄ grasses (Sage et al. 1999).

CONCLUSIONS

The number of similarities between California and Arizona are matched by the differences

between these two regions. The most obvious similarity is that these plant communities share most of the same dominant species as well as a number of genera. The most prominent dissimilarity is that Arizona chaparral has both a spring growing season and a fall growing season which results in two very different postfire floras. Other dissimilarities include the prominence of perennial grasses in Arizona, which is promoted by the summer rains and perhaps by more open shrublands. This life form is largely nonexistent in California postfire chaparral because spring annuals are far better at persisting in landscapes dominated by a long summer drought and the closed canopy chaparral in California excludes herbaceous species to a greater degree than in Arizona. Thus, the primary differences are seen in the herbaceous component of these plant communities and are largely driven by summer rains in one region and absence in another.

The results from this study have implications for paleoecological reconstructions. Palaeocommunities are commonly reconstructed from macrofossils and generally these are restricted to the woody component of the community because herbaceous species are seldom preserved. Based on the woody component of the contemporary California and Arizona communities one would conclude that these are similar plant communities. However, the detailed community characterization demonstrated in this paper shows that these are radically different communities. When confronted with the dual fall and spring herbaceous communities and the major contribution of C₄ perennial grasses to the Arizona postfire community one must conclude that these two regions are dominated by quite different plant communities. Thus, paleofloras reconstructed from just the woody components would be potentially misleading in comparisons of these types of communities.

This is relevant to reconstructing the past history of chaparral as it appears that it originated under summer rain conditions, apparently in the southwestern portion of North America (Ackerly 2009; Keeley et al. 2012). If the Arizona chaparral is a reflection of earlier chaparral stages it strongly suggests that the primary similarity is in the woody flora. The contemporary postfire herbaceous flora in California chaparral appears to be a flora, with similarities to winter rain floras from Arizona chaparral, but largely missing the fall floras of Arizona chaparral. Although lacking in diversity of functional types, the Mediterranean-type climate appears to have played a role in adding to the diversification of the winter rain postfire flora. Many of the genera common in the spring floras of both regions have much greater diversity in California than in Arizona.

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APPENDIX 1

Plant families recorded from just Arizona or just California postfire sites, and families recorded from sites in both regions.

Only in Arizona (19)

Acanthaceae
Aceraceae
Aizoaceae
Asclepiadaceae
Cactaceae
Commelinaceae
Fouquieriaceae
Juglandaceae
Krameriaceae
Linaceae
Lythraceae
Molluginaceae
Pedaliaceae
Pinaceae
Plantaginaceae
Polygalaceae
Verbenaceae
Violaceae
Zygophyllaceae

Only in California (9)

Cistaceae
Crassulaceae
Fumariaceae
Grossulariaceae
Orchidaceae
Orobanchaceae
Rutaceae
Sterculiaceae
Styracaceae

In both Arizona & California (44)

Agavaceae
Amaranthaceae
Anacardiaceae
Apiaceae
Asteraceae
Boraginaceae
Brassicaceae
Campanulaceae
Caprifoliaceae
Caryophyllaceae
Chenopodiaceae
Convolvulaceae
Cupressaceae
Cuscutaceae
Cyperaceae
Ericaceae
Euphorbiaceae
Fabaceae

Fagaceae
Fumariaceae
Garryaceae
Gentianaceae
Geraniaceae
Hydrophyllaceae
Lamiaceae
Liliaceae
Loasaceae
Malvaceae
Nyctaginaceae
Onagraceae
Papaveraceae
Poaceae
Polemoniaceae
Polygonaceae
Portulacaceae
Primulaceae
Pteridaceae
Ranunculaceae
Rhamnaceae
Rosaceae
Rubiaceae
Scrophulariaceae
Selaginellaceae
Solanaceae

APPENDIX 2

Plant genera recorded from just Arizona or just California postfire sites, and genera recorded from sites in both regions.

Only in Arizona (148)

Abutilon
Acacia
Acalypha
Acer
Adiantum
Aeschynomene
Agave
Agropyron
Alternanthera
Androsace
Anemone
Anisacanthus
Anoda
Astrolepis
Bahia
Baileya
Bidens
Boerhavia
Bothriochloa
Bouchea
Bouteloua
Brickellia
Bulbostylis
Calliandra
Carmentia
Cathestecium
Chaetopappa
Chamaecrista
Cheilanthes
Chloris
Commelina
Condalia
Corydalis

Crotalaria
Crusea
Cuphea
Cylindropuntia
Cynanchum
Cynodon
Cyperus
Dalea
Dasyilirion
Dasyochloa
Desmanthus
Desmodium
Dichiptera
Digitaria
Diodia
Ditaxis
Drymaria
Dyschoriste
Dyssodia
Echinocereus
Elionurus
Enneapogon
Ephedra
Epilobium
Eragrostis
Eriastrum
Ericameria
Euphorbia
Evolvulus
Fallugia
Ferocactus
Fouquieria
Funastrum
Geraea
Glandularia
Gomphrena
Guilleminea
Gymnosperma
Hackelochloa
Hedeoma
Helioomeris
Heliotropium
Heteropogon
Heterosperma
Houstonia
Hymenopappus
Hymenothrix
Hymenoxys
Ipomoea
Ipomopsis
Isocoma
Juniperus
Krameria
Laemecia
Lappula
Lasianthaea
Leptochloa
Lycurus
Machaeranthe
Macroptilium
Macrosiphon
Mammillaria
Marina
Melampodium
Melinis
Microsteris
Mimosa
Mitracarpus

Mollugo
Monolepis
Myosurus
Nolina
Notholaena
Oreochrysum
Panicum
Pectis
Pemellia
Phaseolus
Physalis
Pinus
Piptochaetium
Platyopuntia
Portulaca
Proboscidea
Prosopis
Pseudognaphia
Psilactis
Psoralidium
Sanvitalia
Schistophrag
Schoenocrambe
Sclerocactus
Scleropogon
Senna
Setaria
Sida
Sorghum
Spermolepis
Sphaeralcea
Sporobolus
Stevia
Swertia
Symphyotrichum
Tagetes
Tephrosia
Tidestromia
Trachypogon
Trachypogon
Trianthema
Triticum
Urochloa
Verbesina
Viguiera
Zephyranthes
Zornia
Only in California (78)
Achnantherum
Acourtia
Adenostoma
Anagallis
Antirrhinum
Apiastrum
Brachypodium
Calyptridium
Calystegia
Camissonia
Caulanthus
Centaurea
Centaurium
Chaenactis
Chamaebatia
Chlorogalum
Chorizanthe
Clarkia
Claytonia
Cneoridium

- Cordylanthus*
Crassula
Cupressus
Delphinium
Dendromecon
Dicentra
Dichondra
Dodecatheon
Emmenanthe
Eriodictyon
Eriophyllum
Eschscholzia
Eucrypta
Filago
Fremontodendron
Gastridium
Hazardia
Helianthemum
Hemizonia
Heteromeles
Hieracium
Hirschfeldia
Horkelia
Hypochoeris
Keckiella
Lepechinia
Leymus
Lonicera
Malacothamnus
Malosma
Marah
Melica
Monardella
Muilla
Nassella
Navarretia
Nemocladus
Orobanche
Osmadenia
Papaver
Pedicularis
Phacelia
Pickeringia
Piperia
Plagiobothrys
Polycarpon
Pterostegia
Ribes
Scrophularia
Scutellaria
Styrax
Tauchsia
Thalictrum
Toxicodendron
Trifolium
Uropappus
Xylococcus
Zigadenus
In both Arizona and California (109)
Agoseris
Agrostis
Allium
Allophyllum
Amaranthus
Ambrosia
Amsinckia
Arabis
Arctostaphylos
Argemone
Aristida
Artemisia
Asclepias
Astragalus
Atriplex
Avena
Baccharis
Bowlesia
Brassica
Bromus
Calandrinia
Calochortus
Capsella
Carex
Castilleja
Ceanothus
Cerastium
Cercocarpus
Chamaesyce
Chenopodium
Cirsium
Claytonia
Conium
Conyza
Cryptantha
Cuscuta
Datura
Daucus
Descurainia
Dichelostemma
Draba
Elymus
Encelia
Erigeron
Eriogonum
Erodium
Galium
Garrya
Gilia
Gutierrezia
Helianthus
Heterotheca
Hordeum
Iris
Juglans
Lactuca
Lathyrus
Layia
Lepidium
Linanthus
Lineria
Linum
Lomatium
Lotus
Lupinus
Malacothrix
Marrubium
Mentzelia
Mimulus
Mirabilis
Monardella
Mulienbergia
Oenothera
Pectocarya
Pellaea
Penstemon
Phacelia

Plagiobothrys
Plantago
Poa
Polygala
Polygonum
Porophyllum
Quercus
Rafinesquia
Rhamnus
Rhus
Salsola
Salvia
Sambucus
Schismus
Selaginella
Senecio

Silene
Sisymbrium
Solanum
Solidago
Sonchus
Stellaria
Stephanomeria
Streptanthus
Stylocline
Thysanocarpus
Trichostema
Triodanis
Vicia
Vulpia
Yabea
Yucca